Vol 33 No 7

BULLETIN

OF THE

TORREY BOTANICAL CLUB

JULY, 1906

Absorption of atmospheric moisture by desert shrubs

VOLNEY MORGAN SPALDING

A large body of more or less conflicting literature has accumulated on the subject of the absorption of water directly from the atmosphere by leaves and other aerial parts of plants. The lack of agreement on this subject, and the fact that desert plants, if any, might be expected to take advantage of this means of adding to their meager water supply, led to an investigation of this subject by the writer, the results of which have appeared in the Botanical Gazette.* Briefly stated, they go to show that certain desert shrubs absorb to a limited extent water that is presented to their leaves and other aerial parts, while others under similar conditions are quite incapable of doing so.

At the time the experiments referred to were in progress no attempt was made to determine whether any of these plants are capable of absorbing water vapor directly from the atmosphere. It was thought that the low relative humidity of the region in which the Desert Botanical Laboratory is situated rendered such a process improbable, or, if it occurred, that it could hardly reach significant proportions. On returning to the laboratory, however, in the fall of 1905, it was learned that the ocotillo, *Fouquieria splendens*, a shrub which exhibits extreme sensitiveness to variations in water supply, and ordinarily casts its leaves in time of drouth, had been in full leaf during the entire summer, notwithstanding the exceptionally slight rainfall, the effects of which were

* SPALDING, V. M. Biological relations of desert shrubs. II. Absorption of water by leaves. Bot. Gaz. **41**: 262–282. 1906.

[The BULLETIN for June 1906 (**33**: 327–365, *pl. 16, 17*) was issued 20 Jl 1906.]

plainly manifest in the dried-up and discolored vegetation around.* Various other species, notably *Parkinsonia microphylla*, *Lycium Berlandieri*, and some others, were also in full leaf, in striking contrast with their condition the year before; and this state of things, coupled with the extraordinary relative humidity, which for months had averaged approximately 60 per cent., as recorded by the hygrograph, suggested as a possible explanation of the long retention of their foliage the capacity of these plants to absorb water vapor directly from the atmosphere.† The prompt reaction of the ocotillo to increase of water supply, whether through root or stem, had already been strikingly shown by the fact that this species may form as many as five distinct leaf-coverings between February and August, "the exciting cause in each instance being an increase in the water supply" (through the root),‡ and also that leaf-formation may be induced in four or five days by artificial irrigation of the stem.§ It seemed worth while, therefore, to institute a special set of experiments in order to determine whether this shrub, and some others with which it is associated, are capable of directly absorbing and utilizing the water vapor of the atmosphere.

The method employed is essentially the same as that adopted in earlier experiments on leaf-absorption. Leaves and other aerial parts were accurately weighed and then kept for varying periods in a nearly saturated atmosphere, after which they were weighed and differences of weight noted.

The accumulation of more or less dew on one side of the receptacle employed in the experiments was taken to indicate a very nearly saturated atmosphere where the plant was placed. No deposition of dew on the surface of the plant was ever noticed, but if in any instance this occurred, the conclusion drawn from the results obtained is thereby strengthened.

Beginning with the ocotillo, two lots of leaves were taken, the

* While the aggregate rainfall for 1905 was 23.18 inches, that for the six months, May to October, inclusive, was only 4.40 inches.

† CANNON, W. A. The effects of high relative humidity on plants. Torreya **6**: 21–25. 1906.

‡ CANNON, W. A. On the transpiration of *Fouquieria splendens*. Bull. Torrey Club **32**: 397–414. 1905.

§ LLOYD, F. E. The artificial induction of leaf-formation in the ocotillo. Torreya **5**: 175–179. 1905.

first wholly green, though showing some loss of turgidity, while the other lot, from another plant, were turning pale, but had not become yellow. There was reason to believe that all were capable of photosynthesis, but that all had reached a condition in which more water could well be utilized. Inspection of the accompanying table (I), however, shows that both lots of leaves failed to gain in

TABLE I. FOUQUIERIA SPLENDENS. OCTOBER 27–28, 1905.

No.	Time.	Weight.	Loss or Gain.		Conditions.
1	10.30 A.M.	9.257G			Weighed soon after gathering. Recorded relative humidity = 25 per cent.
2	10.35 "	10.677			Weighed soon after gathering. Recorded relative humidity = 25 per cent.
1	2.10 P.M.	9.236	0.021	Loss.	After exposure to currents of air in laboratory.
2	2.15 "	10.654	0.023	"	After exposure to currents of air in laboratory.
1	4.10 "	9.234	0.002	"	After exposure to nearly saturated atmosphere.
2	4.15 "	10.652	0.002	"	After exposure to nearly saturated atmosphere.
1	4.40 "	9.231	0.003	"	After exposure to open air of laboratory.
2	4.45 " October 28	10.648	0.004	"	After exposure to open air of laboratory.
1	6.43 A.M.	9.225	0.006	"	After exposure to nearly saturated atmosphere.
2	6.50 "	10.637	0.011	"	After exposure to nearly saturated atmosphere.
1	10.42 "	9.167	0.058	"	After exposure to sunlight in open air.
2	10.33 "	10.558	0.079	"	After exposure to sunlight in open air.
1	3.33 P.M.	9.164	0.003	"	After exposure to nearly saturated atmosphere.
2	3.37 "	10.554	0.004	"	After exposure to nearly saturated atmosphere.

weight during two hours exposure to a nearly saturated atmosphere, and even lost slightly when kept in it over night. Moreover, following exposure to sunshine in the open air for some three hours, during which the two lots lost 0.6 and 0.8 per cent. of their weight respectively, they still failed to show any increase of weight after being kept nearly five hours in a practically saturated atmosphere. It is important, however, to note that in every case, during their stay in moist air, transpiration was reduced to such a degree as to amount essentially to complete suppression.

This experiment, agreeing with others not reported, indicates no capacity on the part of the leaves of *Fouquieria* to absorb water vapor, even after they have lost turgescence, or have turned pale and are almost ready to fall, but it does point to the prompt influence of a moist atmosphere, in checking, or even suppressing, transpiration, as the probably significant factor determining the long retention of its leaves the present year. At this writing, December 12, many individuals of the ocotillo have not been completely defoliated since last March.

In a second experiment with the same species, leafless shoots a

TABLE II. FOUQUIERIA SPLENDENS. NOVEMBER 13–15, 1905.

No.	Time.	Weight.	Loss or Gain.		Conditions.
1	11.58 A.M.	3.858G			Weighed soon after cutting. Recorded relative humidity = 61 per cent.
2	12.05 P.M.	7.738			Weighed soon after cutting.
1	1.20 "	3.856	0.002	Loss.	After exposure to open air of laboratory.
2	1.24 "	7.735	0.003	"	After exposure to open air of laboratory.
1	3.29 "	3.868	0.012	Gain.	After exposure to nearly saturated atmosphere.
2	3.33 "	7.756	0.021	"	After exposure to nearly saturated atmosphere.
	Nov. 14.				
1	9.58 A.M.	3.886	0.018	"	After exposure to nearly saturated atmosphere.
2	10.04 "	7.785	0.029	"	After exposure to nearly saturated atmosphere.
1	12.54 P.M.	3.863	0.023	Loss.	After exposure to open air of laboratory. Recorded relative humidity = 45 per cent.
2	12.57 "	7.750	0.035	"	After exposure to open air of laboratory.
1	2.40 "	3.873	0.010	Gain.	After exposure to nearly saturated atmosphere.
2	2.45 "	7.768	0.018	"	After exposure to nearly saturated atmosphere.
	Nov. 15.				
1	9.55 A.M.	3.836	0.037	Loss.	After exposure to open air of laboratory.
2	10.00 "	7.712	0.056	"	After exposure to open air of laboratory.
1	12.34 P.M.	3.848	0.012	Gain.	After exposure to nearly saturated atmosphere.
2	12.40 "	7.734	0.022	"	After exposure to nearly saturated atmosphere.

few centimeters in length, with their terminal buds, were employed. Table II shows that these shoots gained appreciably in weight in a nearly saturated atmosphere, but rapidly lost more than they had gained when left in an atmosphere the relative humidity of which was registered at 45 and upwards. The experiment was varied by covering the buds of another shoot with vaseline and leaving those of a control shoot untouched. As shown by Table III, the former shoot gained in weight nearly two thirds as much as the control, thus indicating that although the buds share in the process they are not the chief absorbing structure.

TABLE III. FOUQUIERIA SPLENDENS. NOVEMBER 14–15, 1905.

No.	Time.	Weight.	Loss or Gain.		Conditions.
3	10.48 A.M.	5.643G			Weighed soon after cutting.
4	10.54	6.406			Weighed soon after cutting.
3	2.05 P.M.	5.655	0.012	Gain.	After exposure to nearly saturated atmosphere.
4	2.10	6.425	0.019	"	After exposure to nearly saturated atmosphere.
3	2.30	5.650	0.005	Loss.	After exposure to air of laboratory. Recorded relative humidity = 44 per cent.
4	2.33 Nov. 15.	6.417	0.008	"	After exposure to air of laboratory. Recorded relative humidity = 44 per cent.
3	10.09 A.M.	5.618	0.032	Loss.	After exposure to air of laboratory.
4	10.14	6.365	0.052	"	After exposure to air of laboratory.
3	12.46 P.M.	5.629	0.011	Gain.	After exposure to nearly saturated atmosphere.
4	12.50	6.380	0.015	"	After exposure to nearly saturated atmosphere.

But, notwithstanding the fact, thus fully established, that the shoots of *Fouquieria* absorb considerable quantities of water vapor from a saturated atmosphere, it seems entirely unlikely that in nature the leaves receive from the branches any appreciable amount of water as a result. One morning with the recording hygrometer registering the humidity at 72, the branches lost rapidly a large percentage of what they had gained over night in a nearly saturated atmosphere, and this was the usual, rather than exceptional, state of affairs; so that the rapidity with which the branches return to the air the water they have absorbed, even when the humidity is high, seems to preclude the assumption that any, or at least any considerable amount, is passed on by them to the leaves.

It appears, then, in the case of *Fouquieria*, that (1) the leaves do not, even under favorable conditions, absorb water vapor from the atmosphere; (2) the branches are capable of such absorption, as are also the buds, though the latter are not more specially concerned in the process than the former; (3) both shoots and leaves give off water rapidly, not only in a dry atmosphere but also in one of rather high relative humidity; (4) as is well known, this process is checked or practically suspended in an atmosphere nearly or quite saturated with water vapor.

Herein, apparently, lies the explanation of the fact that in spite of the very scanty rainfall of the summer, the ocotillo has remained in leaf during so large a part of the present year. It is not due to absorption of water vapor from the atmosphere, although the relative humidity, during the period of observation, has reached the extraordinary average of approximately 60 per cent., but it is due to the fact that water, which with lower humidity would be given off, has been retained by the plant. While, too, leaf-formation may be induced, as shown by Lloyd, by artificial irrigation of the stems, but not, as far as the present study indicates, by absorption of water vapor from the atmosphere, there results, nevertheless, from a long period of high relative humidity what is apparently of greater advantage to the plant, namely, the retention, for months in succession, of leaves already formed and in condition for productive work. Had the plants been defoliated, as they must have been if lack of rain had been accompanied, as usual, by low relative humidity, even the maximum number of new leaf-coverings, reported by Cannon, if they could have been produced, would probably fall far below the single continuous leaf-covering in productive energy, though this is a matter the settlement of which would involve another and very different line of experimentation.

Experiments similar to those already described were next carried out with *Celtis pallida*, which was remarkably fresh and green, notwithstanding the slight rainfall of the preceding summer. The leaves were found to lose weight rapidly in a dry atmosphere — upwards of 24 per cent. in three hours — and to gain extremely slowly in an atmosphere nearly saturated with water vapor — only eight-tenths to nine-tenths of one per cent. in five hours. Later, after abundant rain, fresh ends of branches, with leaves, lost 31

per cent. of their original weight when left in a desiccator over night, and subsequently gained in two hours barely enough to show that transpiration had been checked and absorption set up. After further drying, and consequent departure from natural conditions, the rate of gain became greater, but the experiments fail to furnish any satisfactory evidence of the absorption of water vapor from the atmosphere by the living parts of this plant before pathological changes have set in.

Experiments of the same kind with the creosote bush, *Covillea tridentata*, were carried on both before and after heavy November rains. The earlier experiments, in which branchlets and leaves that appeared pretty dry, but still normally active, were employed, exhibited a gain of nearly 1 per cent. in two and one half hours, and their surface showed a distinct increase in the stickiness which is due to the mixture of mucilaginous and waxy substances with which they are coated. Later experiments with leaves and shoots much washed by recent rains showed rapid loss of weight in a dry atmosphere, amounting in some cases to ten per cent., while after remaining in a nearly saturated atmosphere over night the gain was only from one-tenth to less than two-tenths of what they had lost.

These and other experiments with *Covillea* indicate on its part a very limited capacity for absorption of water vapor from the atmosphere. None the less such absorption does take place, and it seems highly probable that it is advantageous to the plant. Even if absorption is so slight as merely to balance, or materially reduce transpiration for a time, this may, at a critical period, prolong the life and activity of leaves that would otherwise succumb; and furthermore the spread of the waxy-mucilaginous covering over the leaves, which is manifestly favored by a high percentage of atmospheric moisture, must also materially aid in checking excessive transpiration. A period of high relative humidity, occurring as it did the past summer, coincidently with a prolonged period of light rainfall, would operate in both of these ways to prevent the premature loss of parts actively engaged in photosynthesis. It is apparently impossible, at present, to express these complicated relations quantitatively, but this by no means detracts from their importance in the economy of a plant, which owes its dominant position over wide areas not to a single advantageous structure but to a complex of successful adaptations.

Experiments of the same general character were conducted on *Prosopis*, *Parkinsonia*, *Franseria*, *Atriplex*, *Encelia*, and a number of other perennials which represent the characteristic vegetation of the region. To give these in detail would serve no useful purpose, and the results may be briefly stated as follows: The mesquite (*Prosopis*) absorbs water vapor through its leaves, but at a slow rate. *Parkinsonia microphylla* showed no capacity for absorption of water vapor except as the specimens employed retained their minute scale-leaves, and then only to a very limited extent. *Franseria deltoidea*, *Abutilon incanum* and *Encelia farinosa* all failed to show any gain whatever in a nearly saturated atmosphere until the experiments had been in progress from two to four days. Later some absorption took place, but up to the time when the leaves were plainly passing into a pathological condition the amount absorbed was wholly inadequate to compensate for what had previously been lost or even to restore turgescence.

From the hygroscopic action exhibited by the fronds of *Notholaena* sp., which in dry weather are rolled up, but are unfolded after rain, it was thought that they would probably exhibit some manifest capacity for absorption of atmospheric vapor, and this anticipation was realized, although, as the records show, it would take at least 14 days for the fronds under observation to absorb from a saturated atmosphere what they had lost in twenty hours, and keeping the curled-up fronds for days in a very moist atmosphere was not sufficient to induce their unfolding. Immersing in water was soon followed by their expansion, and partial unfolding was also induced by placing the subterranean parts in water. It appears, then, that with the coming of rain the fronds of *Notholaena* absorb water directly and that this is also accomplished, though with less prompt and complete unfolding, by the subterranean parts. As the plant continues to absorb water from the soil the fronds remain expanded until the water supply diminishes to a point where they begin to curl up. At this point a high percentage of atmospheric moisture would retard the process, thus keeping them unfolded longer than if the relative humidity were less, and maintaining them in an advantageous position for photosynthesis.

A review of the data gathered establishes the fact that of the

twelve species of desert perennials subjected to experiment all exhibit some slight capacity for direct absorption of water vapor from the atmosphere, but in general the amount absorbed is inconsiderable in comparison with that given off in corresponding periods in dry air. As yet there is no evidence that these almost infinitesimal quantities of water are utilized in the body of the plant. The promptness with which the water thus absorbed is returned to the atmosphere suggests rather a superficial process, purely physical in its nature, and of no immediate physiological significance. In any case the present experiments, taken in connection with earlier ones already referred to, show that the net result to the plants found to be capable of absorbing either liquid water or water vapor is plainly much less in the latter than in the former case. Nevertheless, as shown most clearly in the experiments with *Fouquieria* and *Covillea*, a high degree of saturation of the atmosphere, by directly or indirectly preventing excessive transpiration, may be far more advantageous to the plant than a succession of light rains which are insufficient to moisten the soil; the advantage, in this case, being manifested in most striking fashion to the eye in the living green with which these otherwise sombre-hued shrubs of the desert are clothed.

Possibly the most important conclusion to be drawn from this study and a preceding one on leaf-absorption is the patent fact that the roots of desert plants constitute their only reliably active agent in providing a normal water supply. This conclusion, indeed, was to be expected; but it is none the less important to establish, in the face of evidence that might be interpreted otherwise, the capital fact that upon the roots of these desert plants rests practically the entire burden of securing and transmitting the water upon which they depend, and, however far some of them have departed from the habits of present-day mesophytes, they remain in this particular fundamentally unchanged.

DESERT BOTANICAL LABORATORY,
TUCSON, ARIZONA.

The mechanism of seed-dispersal in Polygonum virginianum *

HOWARD SPRAGUE REED AND ISADORE SMOOT

The achenes of *Polygonum virginianum* Linnaeus have a particularly efficient mode of dispersal. The long two-parted styles are persistent and become lignified during the process of development. If, after maturity, these projecting styles are struck by any object with sufficient impact, the achenes are thrown off with force enough to carry them a distance of three or four meters.

During windy weather the tall, slender racemes are blown against each other and against the strong stems of plants like *Phytolacca* and *Sambucus*, with which this species of *Polygonum* is associated. The impact thus produced is sufficient to throw off the mature achenes without the agency of animals. Nevertheless, animals are very efficient means of dissemination, for, if they do touch the trigger-like styles, the achenes are thrown with some force against the body of the animal, where they cling, the sharp, reflexed points of the style (see fig. 1) becoming fixed in the hair, or fleece, and they may thus be carried some distance.

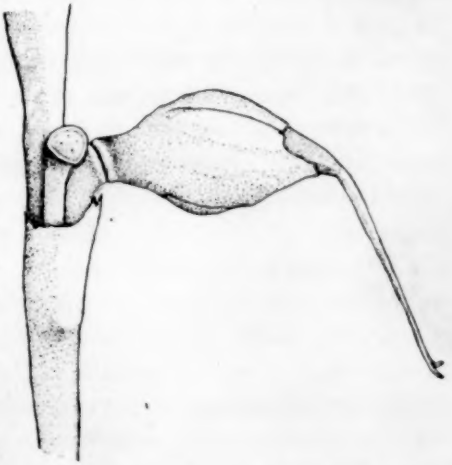

FIG. 1. A mature achene of *Polygonum virginianum*.

All botanical text-books give examples of fruits and seeds which are forcibly ejected when ripe. In most cases the force is due to some property of the ripened wall of the gynoecium. The ejection of the achenes of *Polygonum virginianum* is unique in that the requisite force is derived from a tension in the pedicel.

* Contribution No. 9 from the Botanical Laboratory of the University of Missouri.

Hildebrand ('73) mentions this plant as one whose achenes are transported by animals, but appears not to have noticed their forcible expulsion. He mentions only the hooked styles which fasten the achenes to the hair, or fleece, of animals.

Kerner ('95) described it as a "catapult fruit." He perceived the separation-layer in the pedicel, but gave no satisfactory explanation of the manner in which ejection was accomplished. His account (**2**: 842) might lead one to think that the tension was produced by the cells of the cortical parenchyma. We have not found it to be so.

The devices of the plant for dispersing its fruits have been noted by Beal ('98), but no explanation was given.

This paper relates the results of a histological study of the tissues in question. Since the achenes fly off with a force entirely disproportionate to that which strikes them, it may be assumed that there is some tension existing in the pedicels which, when released, throws the achenes from the plant. It has been supposed that the existing tension was given by changes in the tissues of the pedicel as they became dry. The attempt was made to discover whether changes might be found in the structure or arrangement of these tissues sufficient to account for the phenomenon of dispersal.

The material studied was collected near Columbia, Missouri, in the autumn of 1904, and during the summer and autumn of 1905. All stages were obtained, from the first formation of the raceme to the mature achene. The killing fluids used were mercuric-bichloride in 95 per cent. alcohol, Mann's picro-corrosive fluid, chrom-acetic acid, and Worcester's killing fluid. The older material was embedded in celloidin and the younger in paraffin. The stains used were fuchsin-iodine-green, iron-alum-haematoxylin and safranin, and Delafield's haematoxylin.

P. virginianum constitutes the only member of the subgenus *Tovara*, according to Small ('95). The plants are herbaceous annuals, somewhat woody at the base. When the species of this genus are arranged according to their histological structure, *P. virginianum* appears to stand about midway in the series. The epidermis, like that of nearly all the other species, consists of a single row of cells. The hypodermal tissues are not so well developed

as in those species, like *P. alpinum*, which grow in dry situations, but is better develeped than in species like *P. scandens*, which grow in wet localities. In comparison with the other species, the stereome cylinder of *P. virginianum* is compact and well developed. The elements are small and very thick-walled, therefore they may be regarded as contributing much of the rigidity necessary to support these tall, slender stems.

The phloem bundles, although small, do not disintegrate as they do in some other species. The xylem forms a comparatively wide zone and contributes a great deal of mechanical strength to the stem. It consists of five different elements, namely, woody fibers, tracheids, spiral vessels, annular vessels, and wood parenchyma which gradually merges into the pith.

The pith consists of large cells, hexagonal in longitudinal section. Unlike the same kind of cells in other species, they are usually broader than they are high.

In a general way, the form and structure of the tissues in the pedicel are similar to those in the stem. The most constant difference between them is that some of the individual elements of the pedicels are more elongated than the corresponding elements in the stems. About 0.75 mm. below the base of the achene, the tissues of the mature pedicel are interrupted by a crescent-shaped "separation-layer." It is by virtue of this layer that the fracture is readily effected when the achenes are thrown off. Its characters will be more fully discussed later. The cells of the epidermis, which at first are parallelopipeds, like those of the cauline epidermis, become stretched from four to six times their original length as the pedicel develops.

The zones of stereome and woody tissue are reduced in width and number of elements. The zone of stereome tissue is usually thicker on the concave side of the pedicel than on the convex side (fig. 3). In all probability this may be regarded as a regulatory thickening such as Newcombe ('95) described for mechanical tissues in general.

The fibro-vascular tissue never forms a zone of any considerable thickness. There is no evidence that the phloem bundles ever disintegrate, but are continuous throughout the pedicel, although they decrease in size beyond the separation-layer. Opposite each

phloem bundle there is a group of from five to seven annular and spiral vessels. Between these groups of vessels the space is filled up with wood parenchyma in such a way as to form a continuous cylinder. The woody tissue never reaches any considerable development, hence this cylinder is thin-walled even at maturity.

Just above the separation layer the fibro-vascular bundles branch dichotomously. The outer branches continue their course into the persistent calyx, the inner branches meet and fuse directly below the achene. (Figs. 2 and 3.)

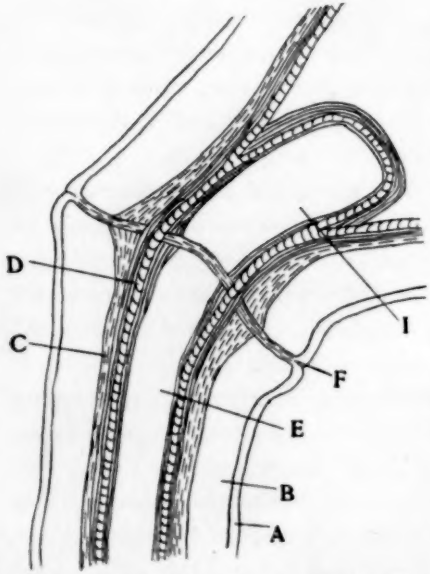

FIG. 2. Diagram of a median longitudinal section of a young pedicel shortly after the differentiation of the separation-layer. *A*, epidermis; *B*, cortex; *C*, sclerenchyma; *D*, fibro-vascular bundles; *E*, pith; *F*, separation-layer; *I*, cushion of thin-walled pith-cells.

A longitudinal section of the pedicel shows that the cells of the pith differ in size and shape from the corresponding cells in the stem. The latter were described as being hexagonal in longitudinal section and distinctly broader than they were high. The pith cells in the pedicels, on the other hand, are rectangular in longitudinal section and have a length from two to six times as great as their width (fig. 5). The longest cells are formed near the base of the pedicel; the shortest ones near the separation-layer. Subsequent changes in the form and structure of the pith cells will be described later.

The achene is attached to the distal end of the pedicel by a broad base, which does not become weakened as the fruit matures. This accounts for the fact that when the achene is cast off the fracture occurs, not at its base, but at the specially developed separation-layer mentioned above.

The wall of the achene consists of two layers. The outer and

thicker layer is composed of compact sclerenchyma elements, which have been described by Sirrine ('94), and the inner layer is composed of long, woody fibers, which are in close contact with the sclerenchyma wall. At the apex of the achene the fibers of the inner wall are continued outward and downward, forming the tissue of the persistent style. The whole structure of the achene gives to it sufficient mechanical strength to resist fracture at all points except the specially constructed separation-layer.

Certain indications of a separation-layer in the pedicel are evident from a very early stage. The youngest flower-stalks ex-

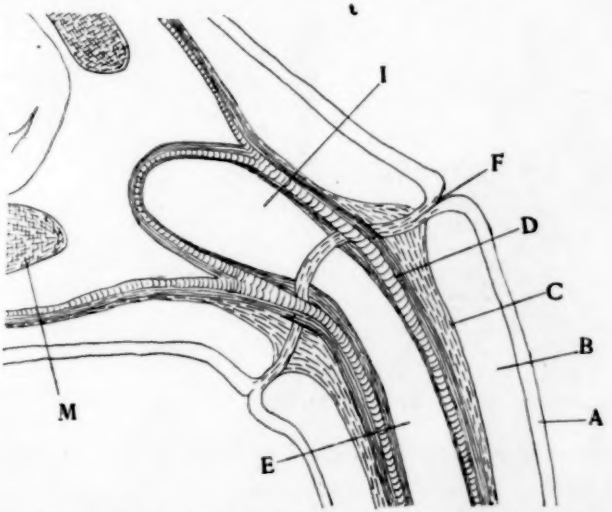

FIG. 3. Diagram of a median longitudinal section of a pedicel at the time of maturity. *A*, epidermis; *B*, cortex; *C*, sclerenchyma; *D*, fibro-vascular bundles; *E*, pith; *F*, separation-layer; *I*, cushion of thin-walled pith-cells; *M*, sclerenchyma-layer of achene-wall.

amined seemed to indicate that the pollen-mother-cells had recently accomplished the second division. In such sections one may discern a zone of short cells extending across the pedicel a short distance beneath the base of the macrosporangium. The cells of this zone are thin-walled and parenchymatous like the other cells of the young pedicel. At the same time, or very shortly afterward, the pedicel is slightly constricted in the region of this zone.

As the flower approaches the time of blossoming the cells of the pedicel undergo differentiation into the tissues described above.

At the time when the gynoecium is pollinated, it has been raised by intercalary growth nearly 0.5 mm. above the place where the zone of short cells arose. Simultaneously, a well-defined separation-layer may be distinguished in the midst of this zone. It consists of two rows of very short cells (fig. 4), which come in contact with the epidermis of the pedicel at the constriction which appeared somewhat earlier. This layer has the general form of a very low, flat-topped dome (fig. 2). All the tissues of the pedicel, except the fibro-vascular bundles, are intersected by this double row of cells. As the superficial notch deepens, the mar-

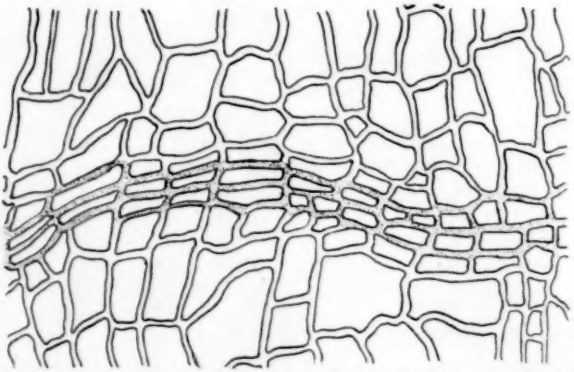

FIG. 4. Section showing the separation-layer shortly after it is differentiated.

gins of these layers are brought into contact with the epidermal layers, and their cells become cutinized.

Following the differentiation of the separation-layer, there is instituted a series of changes in the tissues of the pedicel. The pith-cells for some distance on the proximal side of the layer begin to elongate, and at the same time their walls become considerably thickened. The cell-elongation and wall-thickening appear to start about the same time; ultimately the greatest wall-thickness is reached in the immediate vicinity of the separation-layer. The result is that the separation-layer is pushed upward in the middle, giving it the form of a higher and more sharply pointed dome than formerly (fig. 3). Some notion of the amount of elongation may be formed by noting the increase of curvature in the separation-layer as the time of maturity approaches (figs. 2 and 3). Figure 6, T, represents the thickness of walls of pith-cells in the imme-

diate vicinity of the separation-layer, as compared with the same kind of cells half way down the pedicel, shown in figure 5. On the distal side of the separation-layer, the walls of the pith-cells remain thin and unchanged (fig. 7), except for a few rows in the immediate vicinity of the layer. The slender, pointed cells of this tissue are interpreted to mean that they have grown under pressure, which caused them to glide between neighboring cells, as opportunity offered. The pressure involved was produced by the elongation of the thick-walled cells. By referring to figure 5 it will be seen that the rigid, thick-walled cells of the pith do not glide between each other. The mechanical tissues develop regularly and form the cylinder described above.

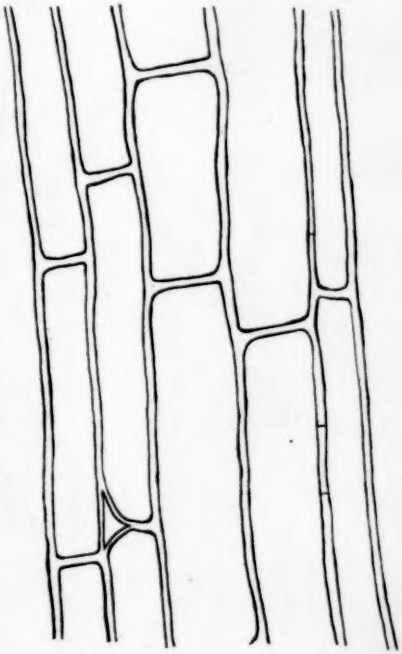

FIG. 5. Longitudinal section of pith taken about midway between the base and apex of the pedicel.

The fibro-vascular system may be compared to a thin-walled, inelastic cylinder (fig. 3, D), inside of which the elongating pith-cells (fig. 3, E) act like a piston moving against the soft, spongy, pith-cells (fig. 3, I) in the closed end of the rigid cylinder. The cushion of thin-walled cells is thus analogous to a compressed spring (one end of which presses against the achene and the other against the separation-layer). So long as the structure is undisturbed, the fibro-vascular cylinder restrains the elongating force of the pith column, but when the rigid style is struck by sufficient force, the strained walls of the cylinder break at the separation-layer and the compressed cushion of cells, suddenly expanding like a released spring, throws the achene off with considerable force. The invariable breaking of the fibrovascular bundles at the separation-layer is not hard to explain. An examination of a

longitudinal section (fig. 3) shows that the reinforcing sclerenchyma-tissue is intersected by the separation-layer, thus materially weakening the mechanical tissue at that point.

Many longitudinal sections show a splitting of the marginal portion of the separation-layer as the fruits approach maturity. This was interpreted to mean that the cells of the cortex had lost part of their water content, and consequently had shrunken. When the cortical layer is thus cleft, the subsequent ejection of the

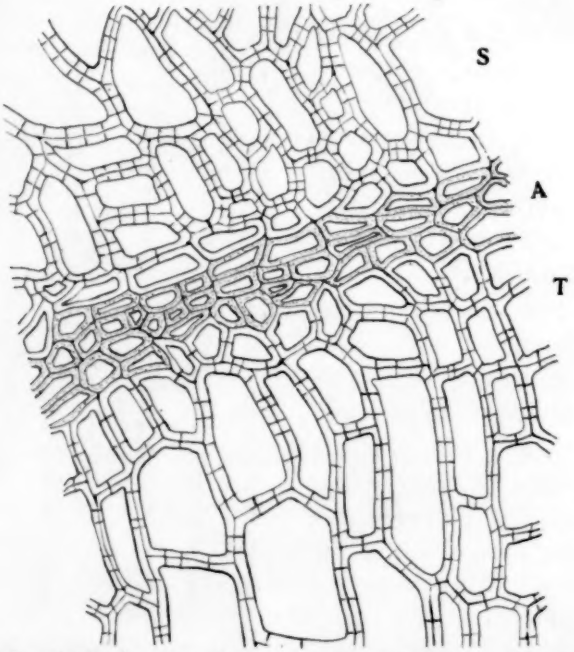

FIG. 6. Longitudinal section of pith at the separation-layer. *A*, separation-layer; *S*, pith-cells on distal side of separation-layer; *T*, pith-cells on proximal side of separation-layer.

achene is entirely dependent on the pith and mechanical tissue. The careful examination of several hundred sections failed to give any evidence which would confirm Kerner's statement that the cells of the cortical parenchyma become lignified. On the contrary, we found that the cortex plays no part whatever in producing the tension which ejects the fruit.

In order to learn whether any of the tissues of the pedicel were hygroscopic, they were subjected to moisture, with subse-

quent drying. Several mature racemes were placed in a moist chamber with a saturated atmosphere and allowed to remain there for four days, during which time the achenes remained attached. The racemes were then removed and placed in an oven, heated to

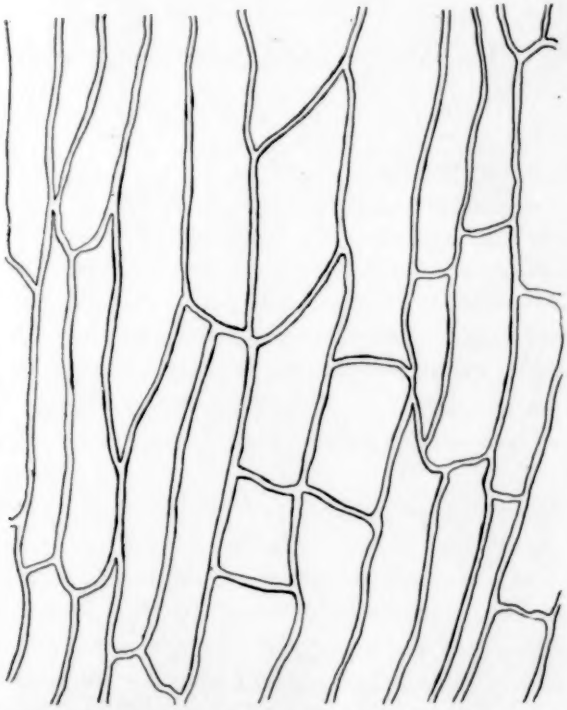

FIG. 7. Longitudinal section of thin-walled pith-cells which form the cushion (*cf.* figures 2 and 3, *I*).

75 degrees C. After seven hours they were again examined, but the effect of the drying had not been sufficient to detach any of the achenes.

The phenomenon of dispersal awaits an impact strong enough to break the fibrovascular cylinder and release the compressed cushion of cells. It is principally dependent on three things — a specially developed "separation-layer"; the existence of a longitudinal tension between the pith-column and the investing fibrovascular cylinder; and a blow on the achene analogous to the pull on the trigger which discharges a gun.

UNIVERSITY OF MISSOURI,
COLUMBIA, MISSOURI.

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The pedunculate species of Trillium

HENRY ALLAN GLEASON

About forty specific names and a correspondingly large number of varietal ones have been proposed for the pedunculate species of *Trillium* during the century and a half that has elapsed since the publication of the *Species Plantarum*. Linnaeus himself left the genus in some confusion by including two species under the name *T. cernuum*. Others added to it by imperfect descriptions and incorrect citations, and Rafinesque complicated matters still further by the publication of a large number of species the identity of which will probably never be satisfactorily established. Gray, Watson, and Harbison have all contributed in bringing order into the genus, and more recently Rendle has published such careful descriptions of the types of the Linnaean species that they are no longer in doubt.

The species fall into three very natural groups separated by the character of the stigmas and ovary. In the first of these, which may be designated the *T. erectum* type, the ovary is deeply and sharply six-lobed, and the members of each pair of lobes, corresponding with one of the three carpels, unite above into a short thick sessile recurved stigma,which tapers gradually to the tip. In the second, the *T. grandiflorum* type, the ovary is less deeply angled or even merely three-lobed; it is truncate, rounded, or somewhat narrowed at the end; and the stigmas are slender and of virtually uniform diameter throughout. *T. rivale* S. Watson is included in this group because of Watson's statement that it is related to *T. nivale*. The material available for examination was too fragmentary to determine accurately the character of the stigma. In the last, or *T. Catesbaei* type, the stigmas are likewise slender and of uniform diameter, but they are united below into a definite style. These distinctions are not only constant, but they are very striking, and characters of no greater importance have been used in other families for the segregation of genera.

Within the three groups thus separated by the structure of the

stigmas, the species are distinguished most certainly by the length of the filaments and anthers, supplemented by the color of the petals and ovary, and the length and position of the peduncle. The absolute length of the stamens may be lessened considerably by drying, but in that case the shrinkage is uniform, so that the proportionate lengths of filaments and anthers remain unchanged. The other specific characters, while quite typical of many species, are either subject to considerable variation in nature or are easily altered by pressing. The color of the ovary, for certain forms at least, is quite constant. A very few species, such as *T. undulatum* and *T. nivale*, may be distinguished by the shape of the leaves, but in general the leaves and stems of all the species are very similar.

No attempt has been made to provide exhaustive descriptions of the species. In some cases the characters used in the key include all of the typical features; in other cases a few additional descriptive notes have been added in the text.

Key to the species

Stigmas sessile, short, stout, tapering from the base to the apex, recurved at the tip, their length about half that of the 6-angled or 6-winged ovary.
North American species; petals white, pink, or dark purple.
Ovary white or with a tinge of pink; petals white or rarely pink; peduncle nodding or horizontal.
Filaments one half as long as the anthers, or shorter. 1. *T. declinatum.*
Filaments two thirds as long as the anthers, or longer. 2. *T. cernuum.*
Ovary dark-purple or nearly black; petals white to dark-purple; peduncle erect or declined, or rarely nodding.
Filaments 8–12 mm. long, approximately equaling the anthers. 3. *T. Vaseyi.*
Filaments 2–6 mm. long, shorter than the anthers or very rarely subequal to them.
Stamens 15 mm. long or more, much exceeding the stigmas. 4. *T. simile.*
Stamens 13 mm. long or less, equaling or shorter than the stigmas.
Anthers purple, 8–10 mm. long, 2–3 times as long as the filaments. 5. *T. Rugelii.*
Anthers yellow, 5–9 mm. long, 1.2–2 times as long as the filaments. 6. *T. erectum.*
Species of eastern Asia and Japan; petals white or none.

Petals none or abortive. 7. *T. Smallii.*
Petals present.
Anthers about equaling the filaments, 4–6.5 mm. long. 8. *T. Tschonoskii.*
Anthers 2–3 times as long as the filaments, about 10 mm. long. 9. *T. camschatcense.*
Stigmas sessile, usually more than half as long as the ovary, slender and of uniform diameter throughout, erect or spreading, or somewhat recurved.
Ovary 3-lobed.
Petals very narrow, less than half as wide as the sepals. 10. *T. Govanianum.*
Petals much broader than the sepals.
Ovary tapering at the tip; peduncle exceeding the leaves. 11. *T. rivale.*
Ovary truncate or rounded; peduncle shorter than the leaves.
Leaves oblong, acute. 12. *T. nivale.*
Leaves ovate, acuminate. 13. *T. undulatum.*
Ovary 6-angled.
Filaments one-half to two-thirds as long as the anthers. 14. *T. Scouleri.*
Filaments equaling the anthers, or barely shorter than them.
Stamens 15 mm. long or more; stigmas straight or nearly so. 15. *T. grandiflorum.*
Stamens 13 mm. long or less; stigmas more or less recurved. 16. *T. ovatum.*
Stigmas united below into a short straight style.
Leaves narrowly elliptic; peduncle erect; stamens straight. 17. *T. pusillum.*
Leaves broadly elliptic; peduncle nodding; stamens curved.
Filaments equaling the anthers. 18. *T. Catesbaei.*
Filaments much shorter than the anthers. 19. *T. affine.*

1. **Trillium declinatum** (A. Gray) sp. nov.

Trillium erectum declinatum A. Gray, Man. ed. 5. 523. 1878.

Stem stout, smooth, erect, 2–3.5 dm. high; leaves broadly rhomboid, 8–12 cm. long and wide, narrowed at base, abruptly short-acuminate; peduncles horizontal or declined, 4–6 cm. long; petals ovate-oblong, white, 2–3.5 cm. long; filaments 2–5 mm. long, 30–50 per cent. as long as the anthers, which are 5–12 mm. long; ovary white or with a tinge of pink, deeply 6-winged; stigmas sessile, stout, thick at the base, tapering gradually to the recurved tip.

Type locality: Ohio.

Distribution: Ohio and southern Michigan to Missouri and southern Minnesota.

Trillium declinatum has heretofore been associated with *T. erectum*, but its affinities, as shown by distribution and structure, are much more with *T. cernuum*. *T. declinatum* also has a pleasant odor, wholly unlike the heavy, disagreeable odor of *T. erectum*.

2. TRILLIUM CERNUUM L. Sp. Pl. 339. 1753

Not *Trillium cernuum* Walt. Fl. Car. 126. 1788, nor Michx. Fl. Bor. Am. 1: 216. 1803.

Peduncle deflexed, 1–4 cm. long; filaments 3–6 mm. long, 67–120 per cent. as long as the anthers, which are 3–6.5 mm. long.

Type locality: Carolina.

Distribution: Nova Scotia to Manitoba; south to Minnesota, Michigan and Pennsylvania, and in the mountains to North Carolina and Georgia. This range lies entirely to the north and east of that of the preceding species, and the only herbarium evidence that they overlap at any place is from collections of both species made in the vicinity of St. Paul, Minnesota.

The most evident distinction between the two in fresh material is the position and length of the peduncle, nodding and short in *T. cernuum*, long and horizontal in *T. declinatum*. The length cannot be taken as an absolute criterion, since in exceptional cases it may fall within the normal limits of the other species, and the position may be changed by pressing. In dried material a safe character is the relative length of the filaments and anthers. Careful measurements of a large series of specimens show that in this the two species do not overlap, and the distinction is so obvious that measurements are virtually never necessary.

Linnaeus' description, as is now well known, referred to two species, this and *T. Catesbaei*. The type specimen, preserved in the Linnaean herbarium, is of the form usually regarded as *T. cernuum*, as has been recently shown by Rendle.

3. TRILLIUM VASEYI Harbison, Biltmore Bot. Studies 1: 24. 1901

Peduncle declined or horizontal, 5–8 cm. long; petals dark-red, ovate, 3.5–6 cm. long, 2.5–4 cm. wide; stamens much surpassing the stigmas; filaments and anthers about equal, each 8–12 mm. long.

Type locality: The southern Alleghanies.

Distribution: The lower Appalachian region, from Tennessee to Georgia and South Carolina.

The flowers are larger and the filaments longer in this than in any other red-flowered North American species.

4. **Trillium simile** sp. nov.

Stem stout, erect, smooth, 3–4.5 dm. high; leaves very broadly rhomboid, abruptly narrowed at base, short-acuminate at apex, 10–18 cm. long and broad; peduncle 3–7 cm. long, declined or cernuous; petals white, broadly ovate, obtuse or subacute, 3–4 cm. long, 2–3 cm. wide; stamens much surpassing the stigmas; filaments 5–6 mm. long, about half as long as the yellow anthers, which are 10–12 mm. long; ovary dark-purple, deeply 6-lobed, the stigmas short, stout, sessile, tapering from the base to the recurved tip.

Type collected in moist woodlands near Tryon, North Carolina; *Biltmore Herbarium 14933A*, in the herbarium of the New York Botanical Garden. Other specimens of this species have been collected on Tryon Mountain, North Carolina, and in Fannin County, Georgia, by A. M. Huger, and at Biltmore, North Carolina.

In general habit it resembles closely *T. Rugelii*, but is distinguished by the much longer stamens, the yellow anthers and the proportionately longer filaments.

5. TRILLIUM RUGELII Rendle, Jour. Bot. **39**: 331. 1901

Peduncle about 2 cm. long, nodding: petals broadly ovate, white; filaments 3–3.5 mm. long; anthers purple, 8–10 mm. long.

Type locality: Broad River, North Carolina.

Distribution: The mountains of western North Carolina and northern Georgia. The Georgia record is based on a fruiting plant, *Harper 1891*, from Randolph county.

6. TRILLIUM ERECTUM L. Sp. Pl. 340. 1753

Trillium pendulum Willd. Gesell. Naturf. Berlin Neue Schr. **3**: 421. 1801.

Trillium rhomboideum Michx. Fl. Bor. Am. **1**: 215. 1803.

Trillium rhomboideum album Michx. Fl. Bor. Am. **1**: 215. 1803.

Trillium foetidum Salisb. Parad. Lond. *pl. 35.* 1806.
Trillium obovatum Pursh, Fl. Am. Sept. 245. 1814.
Trillium erectum atropurpureum Pursh, Fl. Am. Sept. 245. 1814.
Trillium erectum album Pursh, Fl. Am. Sept. 245. 1814.
Trillium purpureum Kin; Ell. Sk. **1**: 430. 1817.
Trillium erectum viridiflorum Hook. Bot. Mag. *pl. 3250.* 1833.
Trillium erectum flavum Torr. Fl. New York **2**: 296. 1843.
Trillium album Small, Fl. S. U. S. 278. 1903.

Peduncle 2–8 cm. long, erect or nearly so; petals ovate to narrowly oblong, dark-purple, white or greenish-white; anthers 5–9 mm. long, once and a fourth to twice as long as the filaments.

Type locality: Virginia.

Distribution: New Hampshire to Ontario, south to Pennsylvania, and in the mountains to Virginia, West Virginia and North Carolina; nearly all of its range lies in the Atlantic watershed.

The species is very variable in the color, size, and shape of the petals, but the different forms so intergrade that specific separation is impossible. Of the forms described by Rendle, number 2 apparently refers to the plant described in this paper as *T. declinatum.* A plate of Willdenow's illustrating his *T. pendulum* leaves no doubt of its identity with the white-flowered form of *T. erectum,* but later usage of the name may possibly refer in part to *T. cernuum.* Terms have been somewhat confused so that no distinction is made between a nodding or pendulous peduncle, hanging below the leaves, and a nodding flower upon an erect peduncle. There is some doubt also concerning the species described as *T. obovatum* by Pursh. It had white, obovate petals, and in this resembles *T. grandiflorum,* but various authors have since regarded it as synonymous with *T. erectum,* and it will be so treated here. Under either interpretation it has no bearing on the nomenclature of any species.

7. TRILLIUM SMALLII Maxim. Mel. Biol. **11**: 862. 1883

Petals none or abortive: anthers short, dilated, blunt, about 3–4 mm. long.

Type locality and distribution: Japan.

Rendle would consider this but a form of *T. Tschonoskii,* with reduced or abortive petals. This peculiarity, however, seems to

be constant, and in addition the anthers are totally different from those of *T. Tschonoskii.*

8. TRILLIUM TSCHONOSKII Maxim. Mel. Biol. **11**: 863. 1883

Trillium erectum album A. Gray, in Perry, Narr. Exped. China and Japan **2**: 320. 1856. Not *T. erectum album* Pursh.

Trillium erectum japonicum A. Gray, Mem. Am. Acad. **6**: 413. 1859.

Peduncle usually only 1–4 cm. long; petals white; flower much smaller than in *T. erectum.*

Type locality: Japan.

Distribution: Japan and China.

9. TRILLIUM CAMSCHATCENSE Ker, Bot. Mag. *sub pl. 855.* 1805.

Trillium obovatum Pursh, Fl. Am. Sept. 245, in part. 1814.

Trillium camtschaticum Pallas; Pursh, Fl. Am. Sept. 246, as a synonym. 1814.

Type locality: Kamtschatka.

Distribution: China, Japan, and eastern Siberia.

10. TRILLIUM GOVANIANUM Wall. Cat. no. 812. 1828. — Royle, Illustr. Bot. Himal. 384. *pl. 93. f. 1.* 1839

Trillidium Govanianum Kunth, Enum. Pl. **5**: 120. 1850.

Type locality and distribution: The Himalaya Mountains.

11. TRILLIUM RIVALE S. Watson, Proc. Am. Acad. **20**: 378. 1885

Type locality: California.

Distribution: California and Oregon.

The slender stem and peduncle do not exceed 2 dm. in height; the leaves are 3–5 cm. long and evidently petioled. The material available for examination is in poor condition, and the species is associated with *T. nivale* and *T. undulatum* from Watson's statement alone. The stigma is said to be short, and the ovary narrowed at the tip; in both of these characters it is quite unlike *T. nivale.*

12. TRILLIUM NIVALE Riddell, Syn. Fl. West. St. 93. 1835

Type locality: Central Ohio.

Distribution: Western Pennsylvania to southeastern Minnesota, a range nearly coinciding with that of *T. declinatum*.

13. TRILLIUM UNDULATUM Willd. Gesell. Naturf. Berlin Neue Schr. **3**: 422. 1801

Trillium erythrocarpum Michx. Fl. Bor. Am. **1**: 216. 1803.

Trillium pictum Pursh, Fl. Am. Sept. 244. 1814.

Type locality: Pennsylvania.

Distribution: Nova Scotia to Ontario and Wisconsin, and south in the mountains to South Carolina and Georgia.

14. **Trillium Scouleri** Rydberg, sp. nov.

Trillium grandiflorum Hook. Fl. Bor. Am. **2**: 180, in part. 1839. Not *T. grandiflorum* Salisb.

Trillium obovatum Hook. *loc. cit.* in part. Not *T. obovatum* Pursh.

Stem stout, erect, 2–4 dm. high; leaves broadly rhomboid, 6–12 cm. long and wide, acute or short-acuminate, rounded or truncate at base, closely sessile; peduncle erect or nearly so, 3–5 cm. long; petals ovate-oblong, white, subacute, 3–5 cm. long, 1–2 cm. wide; stamens 13–24 mm. long, equaling or exceeding the stigmas; filaments 5–9 mm. long, about one-half to two-thirds as long as the anthers; stigmas slender, recurved at the tip, erect, or usually divergent, about equaling the ovary.

Type locality: British Columbia.

Distribution: British Columbia to Montana and California.

15. TRILLIUM GRANDIFLORUM (Michx.) Salisb. Parad. Lond. *pl. 1.* 1805

Trillium rhomboideum grandiflorum Michx. Fl. Bor. Am. **1**: 216. 1803.

Trillium erythrocarpum Ker, Bot. Mag. *pl. 855.* 1805. Not *T. erythrocarpum* Michx.

Type locality: The mountains of North Carolina.

Distribution: From Quebec and New England west to Minnesota, and south along the mountains to Florida.

16. TRILLIUM OVATUM Pursh, Fl. Am. Sept. 245. 1814

Trillium californicum Kellogg, Proc. Calif. Acad. **2**: 50. 1863.
Trillium crassifolium Piper, Erythea **7**: 104. 1899.

Type locality: The Columbia River.

Distribution: British Columbia to Montana, Colorado, and California.

The three preceding species constitute a very well-marked natural group closely resembling each other in habit and flower-structure. In the western species the stigmas are usually somewhat spreading, while in *T. grandiflorum* they are normally erect and connivent. The latter is separated also by its geographical distribution. Aside from these the only reliable characters are found in the length of the filaments and anthers. Measurements of a series of herbarium specimens give the following results:

Species.	Filaments.			Anthers.		
	Maximum.	Mean.	Minimum.	Maximum.	Mean.	Minimum.
T. Scouleri.....	9	6.4	5	15	10.8	8
T. grandiflorum ...	11	9.1	6	13	10.4	8
T. ovatum.....	5	4.4	4	7	6.4	5

T. crassifolium Piper is founded on a small form of *T. ovatum* with thickish, shining, broadly ovate, closely sessile leaves. It has no definite morphological character to separate it from Pursh's species.

17. TRILLIUM PUSILLUM Michx. Fl. Bor. Am. **1**: 215. 1803

Trillium pumilum Pursh, Fl. Am. Sept. 245. 1814.
Trillium texanum Buckl. Proc. Acad. Philad. **1860**: 443. 1861.

Type locality: South Carolina.

Distribution: Pine barrens of the southern Atlantic States. The species is little known and very poorly represented in American herbaria.

18. TRILLIUM CATESBAEI Ell. Sk. **1**: 429. 1817

Trillium cernuum L. Sp. Pl. 339, in part. 1753.
Trillium nervosum Ell. Sk. **1**: 429. 1817.
Trillium stylosum Nutt. Gen. 1: 239. 1818.

Type locality: South Carolina.

Distribution: North Carolina and Tennessee to Georgia and Alabama.

19. TRILLIUM AFFINE Rendle, Jour. Bot. **39**: 334. 1901

Type locality and distribution: Georgia.

No specimens have been seen which could be referred to this species, but Rendle's careful description makes it certain that it is quite distinct from *T. Catesbaei.*

SPECIES DUBIAE

The following species were all described by Rafinesque, with usually very imperfect characterizations. Accurate identification of them from the descriptions alone is impossible, although his statements as to the color of the petals make it probable that most of them refer to *T. erectum* or to *T. cernuum.*

Trillium acuminatum, Med. Repos. N. Y. II. **5**: 361. 1808.

Trillium brevipetalum, Med. Fl. **2**: 100. 1830.

Trillium divaricatum, loc. cit. 102.

Trillium flavum, loc. cit. 100.

Trillium hamosum, loc. cit. 101.

Trillium latifolium, loc. cit. 101.

Trillium lirioides, loc. cit. 100.

Trillium nutans, loc. cit. 99.

Trillium obcordatum, loc. cit. 101.

Trillium spatulatum, loc. cit. 101.

COLUMBIA UNIVERSITY.

INDEX TO AMERICAN BOTANICAL LITERATURE
(1906)

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in its broadest sense.

Reviews, and papers which relate exclusively to forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included, and no attempt is made to index the literature of bacteriology. An occasional exception is made in favor of some paper appearing in an American periodical which is devoted wholly to botany. Reprints are not mentioned unless they differ from the original in some important particular. If users of the Index will call the attention of the editor to errors or omissions their kindness will be appreciated.

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Cook, M. T. The disintegrating influences of tropical plants. Plant World **9**: 129–131. *f. 19*. Je 1906.

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